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„Population density and habitat preferences of the Black-cheeked Ant-Tanager *Habia atrimaxillaris*“

Verfasserin

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Abstract

The Pacific tropical lowland forest in the southwestern part of Costa Rica has an extremely diverse avifauna. Our study object the Black-cheeked Ant-Tanager (*Habia atrimaxillaris*) is a highly range-restricted species with a remaining population in the area of Piedras Blancas and Corcovado National Park. It is assumed that the population is decreasing due to habitat loss and fragmentation. We assessed the population density of this species in the vicinity of the Tropical Research Station La Gamba using the method of distance sampling (two survey periods: February-April 2009 and November 2010 to January 2011) and territory mapping (November 2010 to January 2011). Furthermore the point count method and data on vegetation structure were used to study its habitat preferences. Therefore, 40-44 point counts were conducted per census point between 1 November 2008 and 4 October 2010 at the interior of old-growth forest (10 census points), the margin of old-growth forest (10), young secondary forests (5), gallery forest strips connected to and isolated from closed forest (both 10), oil palm plantations (5), fallows (5) and pastures (5). The species' occurrence at old-growth forest sites was then related to forest cover (within a radius of 200 m around census points) and vegetation structure. Black-cheeked Ant-Tanagers were exclusively found in old growth forest where the species' likelihood of occurrence at census points increased with forest cover, canopy cover and density of trees (with diameter at breast height >10 cm). An average population density between 24 and 27 individuals per km² was estimated by distance sampling, which is in accordance with the population size estimated by territory mapping (17-25 birds per km²). Based on these estimates an overall population size of 12,432 to 20,720 birds is predicted for the remaining 592 km² lowland forest area of the Golfo Dulce region. Since the Black-cheeked Ant-Tanager was only recorded in old-growth forest, apparently does not use strips of gallery forests embedded in a human-dominated landscape matrix as stepping stones or corridors and appears to avoid the forest edge, further forest degradation and fragmentation will have a strong negative impact and should be rapidly reduced by adequate conservation measures.

Keywords: Costa Rica, distance sampling, forest cover, forest structure, Piedras Blancas National Park, population size estimate, tropical lowland forest, territory mapping

Zusammenfassung

Der pazifische Tieflandregenwald im Südwesten Costa Ricas hat eine extrem diverse Avifauna. Unser Untersuchungsobjekt die Schwarzwangen-Ameisentangare (*Habia atrimaxillaris*) ist eine Art mit einem sehr kleinen Verbreitungsareal. Die verbleibende Population beschränkt sich weitgehend auf den Piedras-Blancas- und den Corcovado-Nationalpark. Es wird angenommen, dass die Population durch Habitatverlust und Fragmentierung weiter abnimmt. Wir haben die Populationsdichte dieser Tangarenart in der Nähe der Tropenstation La Gamba durch die *Distance-Sampling*-Methode (zwei Aufnahmeperioden: Februar-April 2009 und November 2010 bis Januar 2011) und Territorienkartierung (November 2010 bis Januar 2011) erfasst. Zusätzlich wurden Punktzählungen durchgeführt und Daten zur Vegetationsstruktur erhoben, um Habitatpräferenzen zu untersuchen. Dafür wurden 40-44 Punktzählungen pro Untersuchungspunkt zwischen 1. November 2008 und 4. Oktober 2010 im Inneren des Primärwaldes (10 Untersuchungspunkte), am Rand des Primärwaldes (10), in jungen Sekundärwäldern (5), in mit dem geschlossenen Wald verbundenen (10) und vom Wald isolierten Galeriewäldern (10), in Ölpalmplantagen (5), in Brachen (5) und in Weiden (5) vorgenommen. Das Vorkommen der Art im Primärwald wurde mit der Waldbedeckung (in einem Radius von 200 m um die Untersuchungspunkte) und der Vegetationsstruktur in Beziehung gesetzt. Die Schwarzwangen-Ameisentangare wurde nur im Primärwald gefunden, wo die Wahrscheinlichkeit eines Nachweises mit steigender Waldbedeckung, Kronenschluss und Dichte großer Bäume (Durchmesser in Brusthöhe >10 cm) zunahmen. Durch *Distance Sampling* wurde eine mittlere Populationsdichte zwischen 24 und 27 Individuen pro km^2 geschätzt. Dies deckt sich gut mit der auf der Territorienkartierung basierenden Dichteschätzung auf der Territorienkartierung deckt (17-25 Vögel pro km^2). Überträgt man diese Schätzungen auf die in der Golfo Dulce

Region verbleibende Tieflandregenwaldfläche von 592 km^2, ist von einer aktuellen Popluationsgröße von 12,432 bis 20,720 Vögeln auszugehen. Die Schwarzwangen-Ameisentangare kommt praktisch ausschließlich im Primärwald vor, ist anscheinend nicht in der Lage die in stark vom Menschen überformte Kulturlandschaft eingebettete Galeriewälder als Trittsteine oder Korridore zu nutzen und zeigt die Tendenz den Randbereich geschlossener Wälder zu meiden. Dadurch ist die Wahrscheinlichkeit hoch, dass fortschreitende Störung und Fragmentierung verbleibender Waldflächen die Populationsentwicklung der Art negativ beeinflussen würde. Diesem Umstand sollte durch entsprechende Naturschutzmaßnahmen so schnell wie möglich Einhalt geboten werden.

Schlüsselwörter: Costa Rica, Distance Sampling, Waldbedeckung, Waldstruktur, Populationsgrößenschätzung, Piedras-Blancas-Nationalpark, tropischer Tieflandregenwald, Territorienkartierung

Introduction

To raise people’s awareness of habitat destruction and degradation in tropical forest ecosystems, no stone should be left unturned. The flagship species concept for example is extremely useful to stress the dimension of habitat loss and fragmentation that these parts of the world are undergoing right now, problems representing major threats to global biodiversity (Curran et al., 2004; Huang et al., 2007; Terborgh, 1992). Many studies underlined the importance of habitat loss as serious threat for all kinds of species (Wilcove et al., 1998; Lawton et al., 1998; Fjeldså, 1999; Myers et al., 2000). For 50 percent of all threatened bird species in the Americas it is the only threat, which needs to be managed and prevented (Collar et al., 1997).

Mesoamerica with its character as a melting pot for northern and southern American species was ranked under the 25 primary biodiversity hotspots by Myers et al. (2000). It houses a high percentage of endemic vertebrates and plants. A total of 9% (29 species) of the 327 threatened bird species in the Americas have a distribution restricted to Central America, which only represents a small proportion of the whole continent. In terms of range-restricted birds Costa Rica and Panama have the most diverse species assemblages in the Neotropics (Collar et al., 1997) and they belong to the 15 countries with most restricted-range bird species in the world (García-Moreno et al., 2007). One of the region’s endemic birds, the Black-cheeked Ant-Tanager *Habia atrimaxillaris* (Dwight et al., 1924), has a particularly small distribution range. It only occurs in the lowlands of the Golfo Dulce Region in the southwestern part of Costa Rica (Slud, 1964; Stiles & Skutch, 1989; Garrigues & Dean, 2007). Due to its extremely small distribution range of only about 500 km^2 the species is classified as ‘endangered’ (Aubrecht, 2008; BirdLife International, 2012). How poor the knowledge on the species’ biology is, cannot be better emphasized than by the fact that the first nests of *H. atrimaxillaris* were just found and described recently (Huber et al., 2008; Sandoval & Gallo, 2009). Furthermore, information on the species’ actual conservation status and its habitat preferences is very limited (Aubrecht, 2008; Aubrecht & Schulze, 2008; Sandoval & Gallo, 2009).

Negative effects of human disturbances on forest birds were reported for many tropical regions (Thiollay, 1992; Schulze et al., 2004; Waltert et al., 2005; Gray et al., 2007; Maas et al., 2009; Mordecai et al., 2009). Range-restricted understory birds respond particularly sensitive to anthropogenic forest disturbance (Gray et al., 2007). Therefore, we expect that with ongoing fragmentation of the Pacific lowland forest remaining populations of the endemic Black-cheeked Ant-Tanager will further decline in the next few years. Even well protected areas such as Corcovado National Park are still strongly affected by deforestation close to its boundaries (Arturo Sánchez Azofeifa et al., 2003), which is increasing their isolation from other remaining forest fragments, a phenomenon found to negatively affect most tropical protected areas (Laurance et al., 2012). The range of the Black-cheeked Ant-Tanager declined by approximately 50% since 1960 (BirdLife International, 2012). The only remaining populations are found in Corcovado National Park on the Osa Peninsula and in the vicinity of Golfito, particularly in Esquinas Forest (Piedras Blancas National Park) and the Golfito Faunal Refuge (Schulze & Riedl, 2008; Seaman & Schulze, 2010; BirdLife International, 2012).

Published information on habitat preferences of the Black-cheeked Ant-Tanager indicates that the species is restricted to the understory of dense lowland rainforest (Stiles & Skutch, 1989), where it occurs in undisturbed, older secondary and selectively logged forest areas (e.g. Aubrecht, 2008). However, so far no studies quantitatively analyzed the species' habitat preferences, using a standardized survey design. In contrast to other *Habia* species (e.g. *H. gutturalis* and *H. fuscicauda*), the Black-cheeked Ant-Tanager forages further up in the undergrowth and prefers more mature forest (Willis, 1966).

Depending on the information used for estimating the species' current population size, the total number of birds is ranging between ca. 6,000 and 20,000 individuals (BirdLife International, 2012). In this study, territory mapping and the distance sampling method were used for estimating the species' population density in a part of the Esquinas Forest. So far such data are missing for this forest reserve. Furthermore, we tried to identify important habitats and forest vegetation structures preferred by the Black-cheeked Ant-Tanager. In particular, two main hypotheses were tested: (1) *Habia atrimaxillaris* prefers primary and old-growth secondary forest although it occasionally can be observed in other habitats (e.g. beachfront scrub, palms adjacent to forest) (Stiles & Skutch, 1989; Capper et al., 1998; Aubrecht, 2008). Slud (1964) even noted, they it live more in tall second growth and broken forests than in the interior of unbroken forests. (2) Due to its presumable preference for the understorey of dense lowland forest (Stiles et al., 1989; Aubrecht, 2008), we expect that its occurrence is affected by the extent of forest cover and vegetation structure (e.g. tree density and canopy cover).

Material and methods

Study area

The study area is situated in the Golfo Dulce region in the southwestern part of Costa Rica. The remaining lowland forests in this region are relatively well protected by the Corcovado National Park (established in 1975) located on the Osa Peninsula and the Piedras Blancas National Park (established in 1994) on the eastern side of Golfo Dulce. These two protected areas are connected through the Golfo Dulce Forest Reserve (established in 1979). Furthermore, a corridor project to improve connectivity between these two National Parks and other protected areas in their vicinity is in progress as part of the project for a Mesoamerican Biological corridor (Ankersen et al., 2006).

Our study sizes were located in vicinity of the village La Gamba (N 8°42′30″, W 83°11′0″) and the Tropical Research Station La Gamba (N 8°42′61", W 83°12′97"; Fig. 1). Here, most areas on flat terrain are dominated by human-dominated habitats (pastures, annual cultures, oil palm plantations, settlements) and secondary forest. On hilly terrain, large parts of the study area are still covered with nearly pristine forest (Fig. 1; for a more detailed description of habitat types see Höbinger et al., 2011).

The forest area in immediate vicinity of the Tropical Research Station La Gamba is located between altitudes of 75 and 350 m asl and belongs to the Piedras Blancas National Park. It is easily accessible via an existing trail system with a total length of 9.2 kilometers. The trails are mainly situated in primary forest (76% of total trail length). The rest of the trails are situated in old-growth secondary forest.

The study area has a mean daily temperature of 28.5°C; the annual precipitation is about 6000 mm. The rainy season lasts from August to November, a drier period usually lasts from January to March (Weissenhofer & Huber, 2008a).

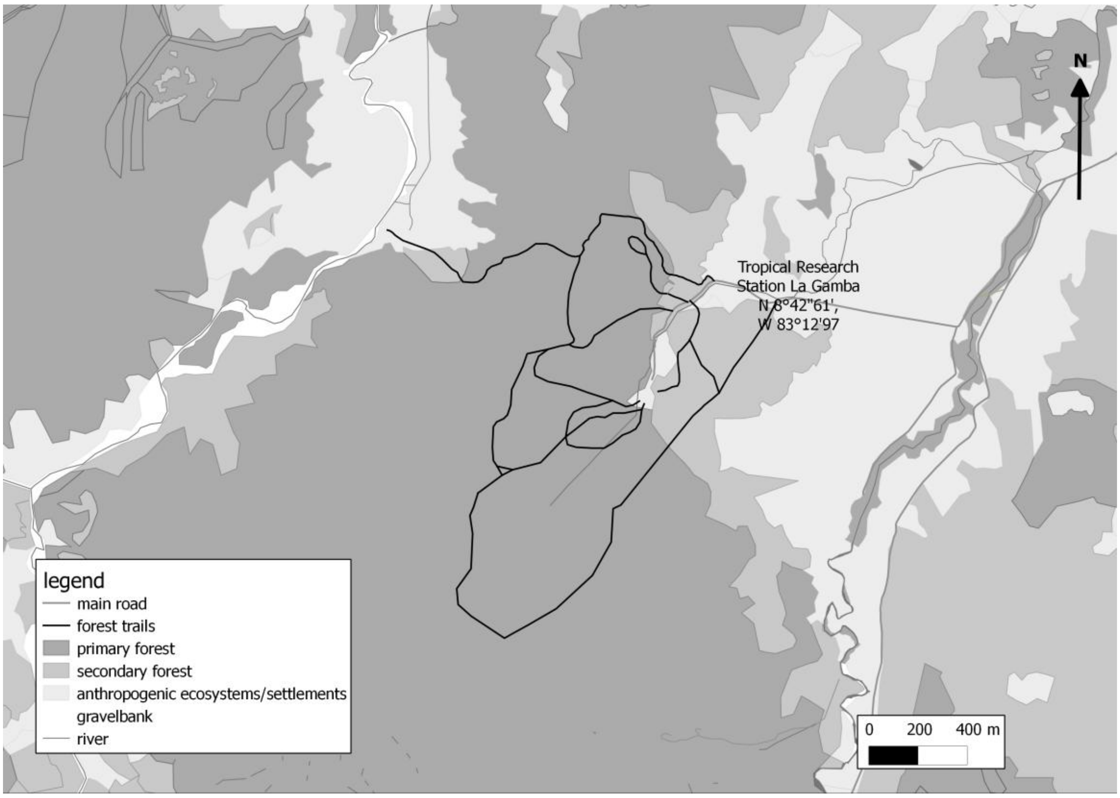

Figure 1. Map of the study area indicating habitat types and the trail system in vicinity of the Tropical Research Station La Gamba.

Although the knowledge on the avifauna of the Golfo Dulce region is far from being comprehensive (Aubrecht & Schulze, 2008), at least an up-to-date checklist of birds is available (Tebb, 2008). Additionally, first studies on the conservation relevance of various habitat types for the region's forest birds have been published (Schulze & Riedl, 2008; Seaman & Schulze, 2010). The high conservation value of the study area is underlined by the occurrence of the Black-cheeked Ant-Tanager (Tebb, 2007).

Point counts

Data of a bird survey along a gradient of forest disturbance and land-use intensity by Isabell Riedl (IR) were used to analyze habitat preferences of the Black-cheeked Ant-Tanager in our study area. To characterize bird assemblages IR conducted point counts in eight different habitats: forest interior (FI) and margin (FM) of old-growth forest, young secondary forest (YSF), gallery forest connected to closed forest (GC) and isolated (GI), oilpalm plantations (PP), fallows (FA) and pastures (PA). For the forest types between ten (FI) and eleven replicate sites (FM, GC, GI) were selected for standardized bird counts (Fig. 2). FI sites were situated within the large forest block of Piedras Blancas National Park, FM sites were located at its edge. FM sites were defined as located within the transition zone between up to ca. 50 m towards the forest interior and (semi-) open human-dominated habitats. Gallery forests were defined as tree strips along streams crossing open areas. When being in direct contact to closed forest, they were classified as “connected“ (GC), otherwise they were defined as “isolated” (GI). The mean length and width (± SD) of forest strips was 923 (± 1154.37) m and 62.05 (± 40.33) m for GC sites and 1974.55 (± 1568.10) m and 21.77 (± 40.33) m for GI sites, respectively. The mean distance (± SD) to the forest margin was 173.73 (± 154.70) m for GC sites and 543.00 (± 141.13) m for GI sites. For all other habitat types (YSF, PP, FA, PA) five replicate sites were selected (Fig. 2).

Field work was conducted by IR between 1 November 2008 and 4 October 2010. At each study site 10-min point counts were performed from dawn (5:00) to 10:00 (e.g. Blake 1992) using a 8x40 binocular. All birds seen or heard within a radius of ca. 25 m around the census points were noted. Each day bird counts were done at 8-12 census points. To avoid that comparisons between sites are biased by temporal differences in detection rates of birds, census points were visited in a rotating order (Blake, 1992). Each census point was visited 10 to 12 times in October-February 2008/2009 and 2009/2010 (both dry season) and in June-September 2009 and 2010 (both rainy season). Only Black-cheeked Ant-Tanager records were used for this study.

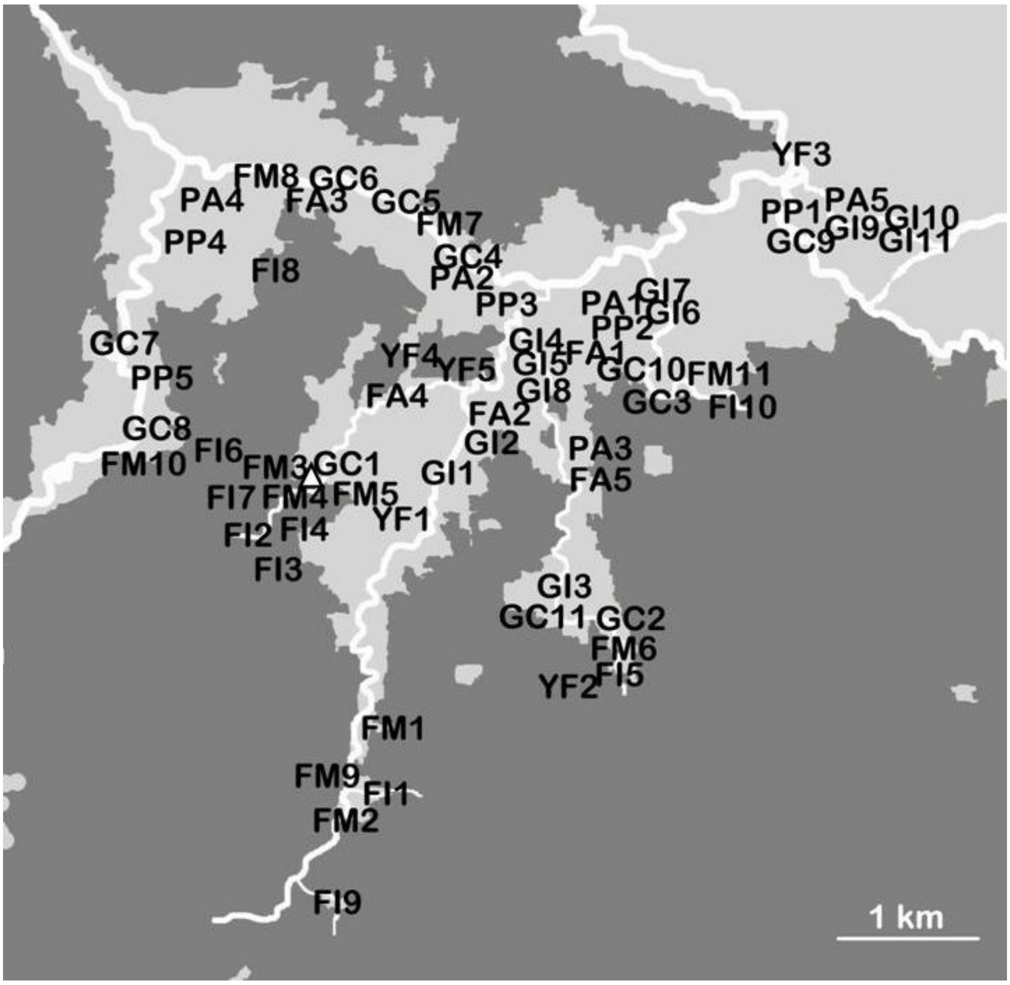

Figure 2. Map indicating census points used for conducting bird surveys in eight different habitats: FI ─ interior of old-growth forest, FM ─ margin of old-growth forest, YSF ─ young secondary forest, GC ─ gallery forest strips connected to closed forest, GI ─ gallery forest strips isolated from closed forest, PP ─ oil palm plantations, FA ─ fallows, PA ─ pastures. Different shading indicates old-growth forest (dark grey), human-dominated habitats (pale grey) and rivers and streams (white). The Tropical Research Station La Gamba is marked by a white triangle.

Habitat variables

To evaluate the importance of edge effects on the occurrence of Black-cheeked Ant-Tanager at old-growth forest sites, for all FI and FM sites forest cover was quantified within a radius of 200 m around census points. Therefore, a digital vegetation map of the study area (Weissenhofer et al., 2008b) which was updated and modified using aerial photographs of 2009 (OpenLayers plugin of Quantum GIS 1.7.2) and ground survey experiences, was used to digitise old-growth forest areas (primary and old-growth secondary forest) in the Geographical Information System Quantum GIS 1.7.2 (Quantum GIS Development Team, 2011). Forest cover was then calculated as the percentage old-growth forest within the 200 m radius around the census points using the software package ArcMap 9.0 (ESRI).

To describe vegetation structure at FI and FM census points we measured or estimated tree density, canopy cover and understory density. Tree density was measured as the number of trees (with diameter at breast height >10 cm) within a radius of 25 m around the census points. To estimate canopy cover four photographs were taken of the canopy in four different directions from the census point at the margin of the 25 m radius. Canopy cover was estimated for each photograph to an accuracy of 10% and then quantified for every census point as the mean of the four estimates. To estimate understory density a photograph was taken from breast height towards the ground at eight randomly selected points within the radius of 25 m around census points. For each of the eight points understory density was estimated as the percentage (to an accuracy of 10%) of the photograph covered by vegetation. Vegetation density at census points was then quantified as the mean of the eight values.

Distance sampling

The method of distance sampling was used to estimate the population density of Black-cheeked Ant-Tanager within old-growth forest. In contrast to traditional bird survey methods, distance sampling is a rather simple approach to estimate population density in a defined area (Thomas et al., 2010). We recorded birds along line transects and measured the perpendicular distance between the transect line and all visually and acoustically detected birds with a rangefinder (Nikon Laser 800 S). There are three main assumptions, which have to be fulfilled to achieve reliable density estimated: (1) Objects on the transect line are detected with certainty, (2) objects are detected before moving and (3) distance measurements are exact (Thomas et al., 2010).

Transects for distance sampling should be random and straight and distance sampling is based on the assumption that the location of detected animals is independent of the positions of the transect lines, which becomes critical if transects are placed along tracks (Thomas et al., 2010). We had to use the existing trail network for the bird survey due to the steep terrain in our study area, which avoided to establish randomly placed transects (Hiby & Krishna, 2001; Gale & Thongaree, 2006). However, it appears that the species did not avoid the forest trails, which were only ca. 1 m wide so that the understory vegetation was only affected to a minor extent. Furthermore, to minimize the impact, we used the edges of those trails as zero-line for measuring perpendicular distances between the transect line and observed birds.

When conducting distance sampling along transect lines, usually 5% of the measured distances are truncated, because they contribute little to the abundance estimate (Buckland et al., 2001). We truncated our distance measurements of detected birds at 60 m. In fact, only two of the detections during the two survey periods have been beyond 50 m. The truncation for our line transect sampling was between 10 and 15% of the maximum detection distance.

There have been two surveys to estimate the population density of Black-cheeked Ant-Tanagers in the study area. The first survey was conducted from February to April 2009 by Julian Fricke and Moritz Katz, the second survey from November 2010 to January 2011 by Jessica Svea Cornils. The whole trail network was divided in subunits which were each surveyed between 9 to 28 times in 2009 and between 8 and 12 times in 2010/2011. This resulted in a total of 168 km transect walks in 2009 and 95 km in 2010/2011. Surveys were done between dawn (5:30 am) and 12:00 pm and between 3:00 pm and dusk (6:00 pm).

Territory mapping

For all Black-cheeked Ant-Tanagers, which were observed during transect walks between November 2010 and January 2011, their location was measured with a GPS device. Quantum GIS map (Quantum GIS 1.7.3, Quantum GIS Development Team, 2011) was then used to visualize the spatial distribution of records and to construct territories. Spatially clustered observations were defined as territory. When clustered observations were over 50 meters apart from each other and/or individuals were observed on the same transect at approximately the same time in different locations, observations were assigned to two different territories. Single observations of solitary birds were not classified as territories. They may represent juvenile birds still searching for new territories or non-breeding "floaters" rather than birds occupying a territory. However, a partly arbitrary interpretation of the spatial distribution of territories cannot be avoided when using such an approach without the marking (e.g. by color rings) of birds.

Data analysis

To compare preferences of Black-cheeked Ant-Tanager for different habitats (FI, FM, YSF, GC, GI, PP, FA, PA), we compared the mean number of birds observed per census point between all habitats. Abundance per census point was quantified as the mean number of birds recorded per 10-min count. Because birds were only observed at FI and FM sites, a t-test was used to test for differences in abundance only between these two forest types.

To test for effects of forest cover, tree density, canopy closure and understory density on the occurrence of Black-cheeked Ant-Tanager univariate logistic regressions were calculated. Subsequently, generalized linear models (GLMs) with binomial error distribution and logit-link function were used to evaluate effects of habitat variables on the species' occurrence at census sites. Before, variables were tested for multicollinearity. In case of significant correlations between habitat variables only these variables were further considered which proved to have a stronger effect on Black-checked Ant-Tanager occurrence in univariate logistic regressions. Then GLMs including all remaining variables and possible subsets were calculated and ranked according to their corrected Akaike Information Criterion (AIC_c) values. AIC_c weights were calculated as a relative measure of support for a model. A higher AIC_c weight indicates a higher relative likelihood of a model compared to alternative models (Wagenmakers & Farrell, 2004). To detect significant effects of habitat variables included in the GLMs, Wald statistics were calculated. All analyses were calculated with the software Statistica 7.1 (Statsoft, Inc., 2005).

Based on the measured perpendicular distances between observed birds and the transect lines, the population density of the Black-cheeked Ant-Tanager was estimated by the software Distance 6.0, which fits a detection function to the observed distances (Bibby et al., 1998; Thomas et al., 2002). The analysis started with a truncation of the data at a distance of 60 m from the transect line. Due to the area's topography and the dense forest understory, at distances of more than 60 m visual and acoustical detections are very unlikely and resulting distance measurements too inaccurate.

Of all the models Distance 6.0 provides, we used the four models, which perform best in many studies (Thomas et al., 2010). To select the two models, which fit best to our data quantil-quantil plots were used by comparing the detection functions of the models with the actual distribution of our distance data (Thomas et al., 2010). Selected models showed the best fit of the data points with the detection function based on a visual evaluation. This selection of models was then additionally cross-checked using the ranking of models according to the Akaike information criterion (Thomas et al., 2010). The population density was estimated separately for the two survey periods 2009 and 2010/2011, and by combining data from both survey periods. Because differences in the size of Black-cheeked Ant-Tanager groups between both survey periods could potentially result in a difference in detectability, we tested if the number of birds per observation differed between both survey periods using a Mann-Whitney U-test, the test was calculated with Statistica 7.1 (Statsoft, Inc., 2005).

Results

Habitat preferences

Our point census data from different habitats ranging from forest interior towards highly modified land-use systems clearly demonstrate that the Black-cheeked Ant-Tanager is restricted to the interior and the margin of old-growth forest (Fig. 3). Although the mean number of birds counted per census point was nearly twice as high at FI than at FM sites it did not differ significantly between both habitats (ttest: $t = 1.26$, df = 19, $p = 0.223$).

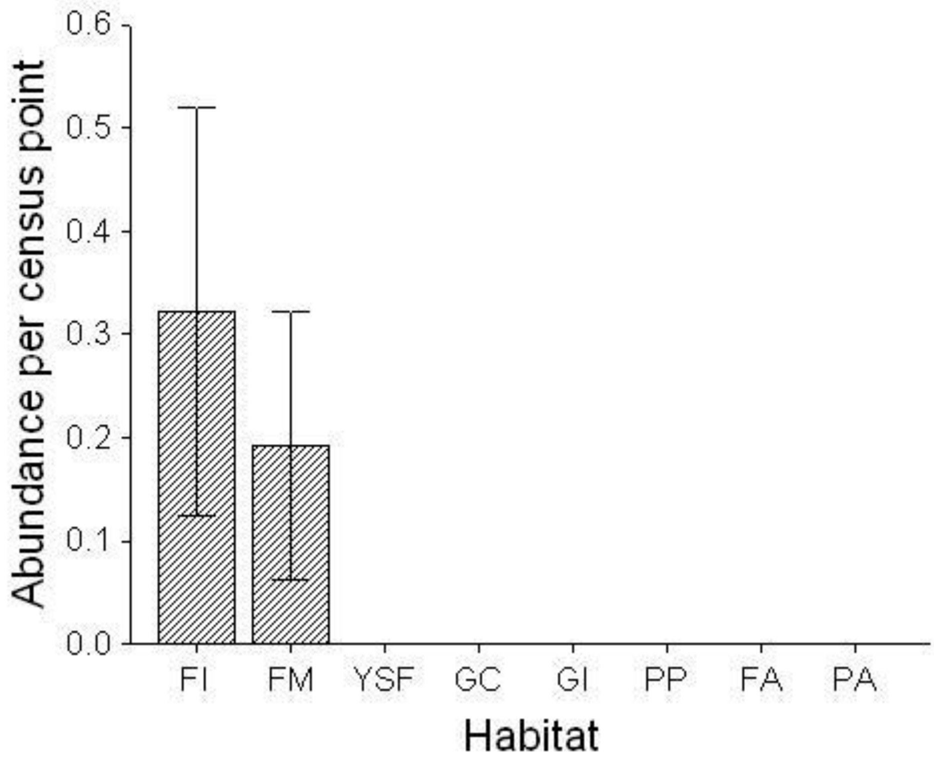

Figure 3. Mean abundance (± 95% CI) of Black-cheeked Ant-Tanager individuals per census point in different habitat types. Abundance at census points was quantified as the mean number of birds observed per 10-min census. Habitat abbreviations: FI — interior of old-growth forest (N = 10 census points), FM — margin of old-growth forest (N = 11), YSF — young secondary forest (N = 5), GC — gallery forest strips connected to closed forest (N = 11), GI — gallery forest strips isolated from closed forest (N = 11), PP — oil palm plantations (N = 5), FA — fallows (N = 5), PA — pastures (N = 5).

Effects of forest cover and vegetation structure at old-growth forest sites

Calculated logistic regressions indicate that the likelihood of Black-cheeked Ant-Tanager occurrence at forest census points increased significantly with increasing forest cover (χ^2 = 6.23, p = 0.013; Fig. 4a), increasing tree density (χ^2 = 7.16, p = 0.007; Fig. 4b) and increasing canopy cover (χ^2 = 5.46, p = 0.019; Fig. 4c). Only understory density did not affect the species' occurrence (χ^2 = 2.28, p = 0.131).

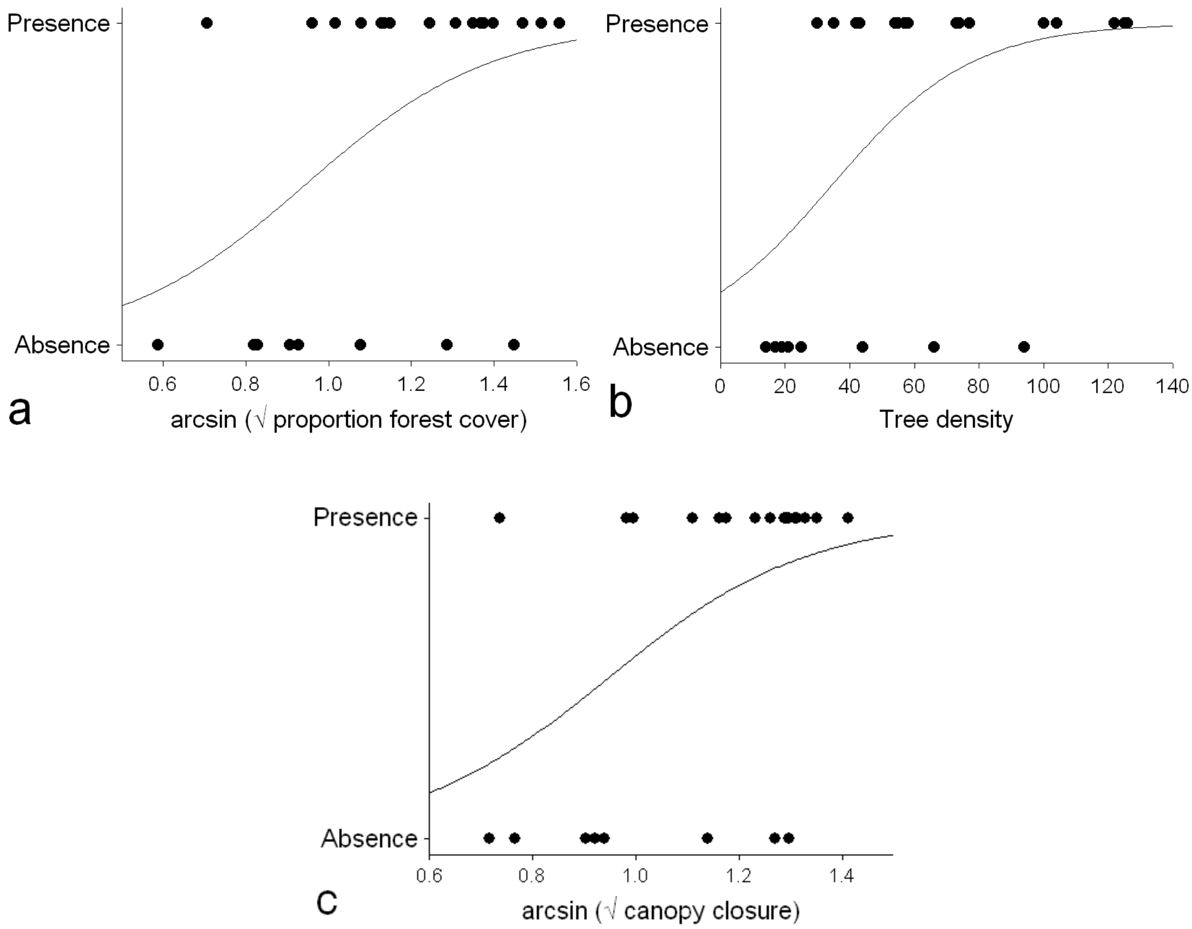

Figure 4. Univariate logistic regressions showing effects of (a) forest cover, (b) tree density and (c) canopy closure on the occurrence of Black-cheeked Ant-Tanager at forest census points (FI and FM sites).

Because tree density and canopy closure were highly correlated ($r = 0.75$, $p < 0.001$), canopy closure was excluded from the subsequently calculated GLMs due to its weaker effect on the occurrence of Black-cheeked Ant-Tanager according to univariate logistic regressions. GLMs calculated with the three remaining habitat parameters and all possible subsets indicate a prominent effect of forest cover on Black-cheeked Ant-Tanager occurrence. This variable remained in all three best models (Table 1) and was the only variable significantly affecting the species' occurrence according to Wald statistics (Table 2).

Table 1. Results of GLMs (with binomial error distribution and logit-link function) calculated to evaluate effects of forest cover (arcsin √x transformed), tree density and canopy cover (arcsin √x transformed) on the occurrence of Black-checked Ant-Tanagers at forest census points (FI and FM sites). GLMs were calculated including all predictor variables and all possible subsets and then ranked according to their corrected Akaike values (AIC_c). Furthermore, AIC_C weights and *p* values are provided for each model.

Included variables	AIC_C	AIC_C weight	*p*
tree density, forest cover	**25.657**	**0.353**	**0.002**
tree density, mean understory density, forest cover	**25.826**	**0.342**	**0.002**
mean understory density, forest cover	**27.265**	**0.158**	**0.004**
tree density	**28.968**	**0.065**	**0.007**
forest cover	**29.901**	**0.041**	**0.013**
tree density, mean understory density	**30.338**	**0.034**	**0.020**
mean understory density	33.853	0.006	0.130

Table 2. Wald statistics from univariate analyses of predictors in GLMs testing for effects of tree density, mean understory density and forest cover on Black-cheeked Ant-Tanager occurrence at forest census points (Table 1). Variables with a significant effect are printed bold.

Variables	Wald Statistic	*p*
tree density	2.453	0.198
mean understory density	1.663	0.117
forest cover	**4.096**	**0.043**

Estimating Black-cheeked Ant-Tanager density by distance sampling

During distance sampling Black-cheeked Ant-Tanagers could be observed 101 times with 185 birds in 2009 and 53 times with a total number of 102 individuals in 2010/2011. The mean group size (± SD) of 1.85 (± 0.96) birds in 2009 and 1.93 (±

0.83) birds in 2010/2011 did not differ significantly (Mann-Whitney U-test: U = 2433.50, p = 0.407) between the two survey periods.

The two distance sampling models which have been pre-selected through the quantil-quantil plots and the Akaike information criterion (AIC) are the hazard rate simple polynomial and the half normal cosine model. Due to their similar AIC values population densities are provided for both models; only difference between AIC values of both models for the 2009 survey were larger than 2 (Table 3). Some of the resulting detection probability curves underestimated the number of observed birds close to the transect line and overestimated the number of detected birds in the next distance band (Fig. 5a-b, e-f). Only the distribution of the detection distances of the 2010/2011 survey is predicted very precisely by the calculated detection probability curves (Fig. 5c-d).

Predicted densities were 22.0% (hazard rate simple polynomial model) and 31.4% (half normal cosine model) higher for 2010/2011 than 2009. When data from both survey periods was combined population densities reached values intermediate between the densities estimated for the first and second survey period. Five of the six models estimated Black-cheeked Ant-Tanager densities between ca. 21 and 27 individuals per km^2. A much higher density of ca. 35.6 birds per km^2 was estimated for 2010/2011 by the half normal cosine model (Table 3).

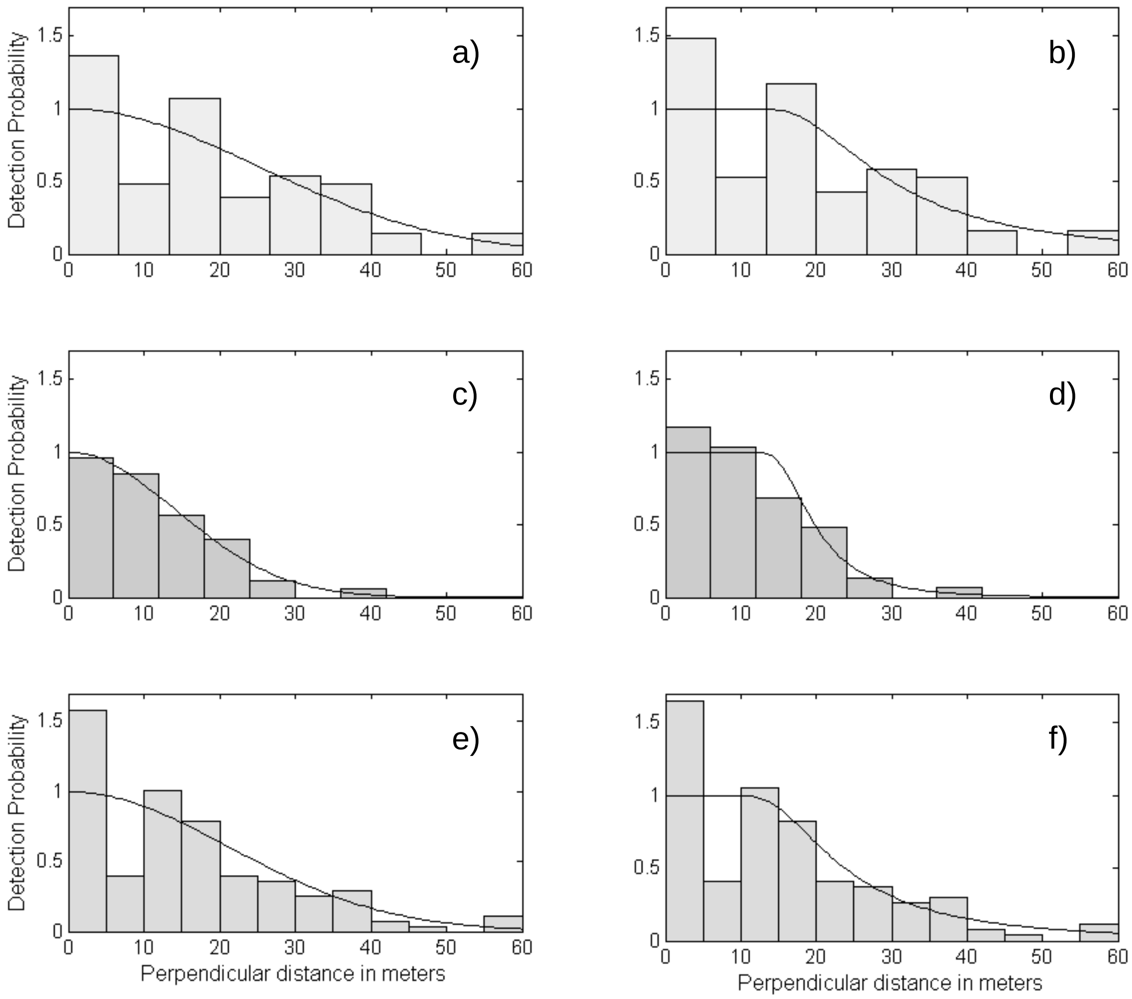

Figure 5. Histograms of detection distances for the transect surveys conducted in (a-b) 2009 and (c-d) 2010/2011 and (e-f) for a combination of both survey periods. Also shown are the corresponding fits of models predicting the detection probability with increasing distance from the transect line using a truncation at 60 m distance from the transect line. Detection curves in graphs on the left side are predicted by hazard rate simple polynomial model and on the right side by half normal cosine model.

Table 3. Akaike information criterion (AIC) values for two different models used to estimate the population density (birds/km^2) of Black-cheeked Ant-Tanager for the survey periods 2009 and 2010/2010 and for both survey periods combined.

Model	Survey period 2009		Survey period 2010/2011		Both survey periods	
	AIC	birds / km²	AIC	birds / km²	AIC	birds / km²
Hazard rate simple polynomial model	740.52	21.08	354.42	27.04	1106.96	24.34
Half normal cosine model	737.75	24.43	352.42	35.59	1105.26	26.51

Estimating Black-cheeked Ant-Tanager density by territory mapping

A total of twelve territories were identified in our study area. Three single observations were not assigned to a territory (Fig. 6). Assuming that territories are occupied by a pair or a pair and at least one juvenile bird a population density of 17 and 25 birds per km^2, respectively, was estimated by territory mapping for our study area of 1.45 km² (100 m buffer zone on both sides of the transects).

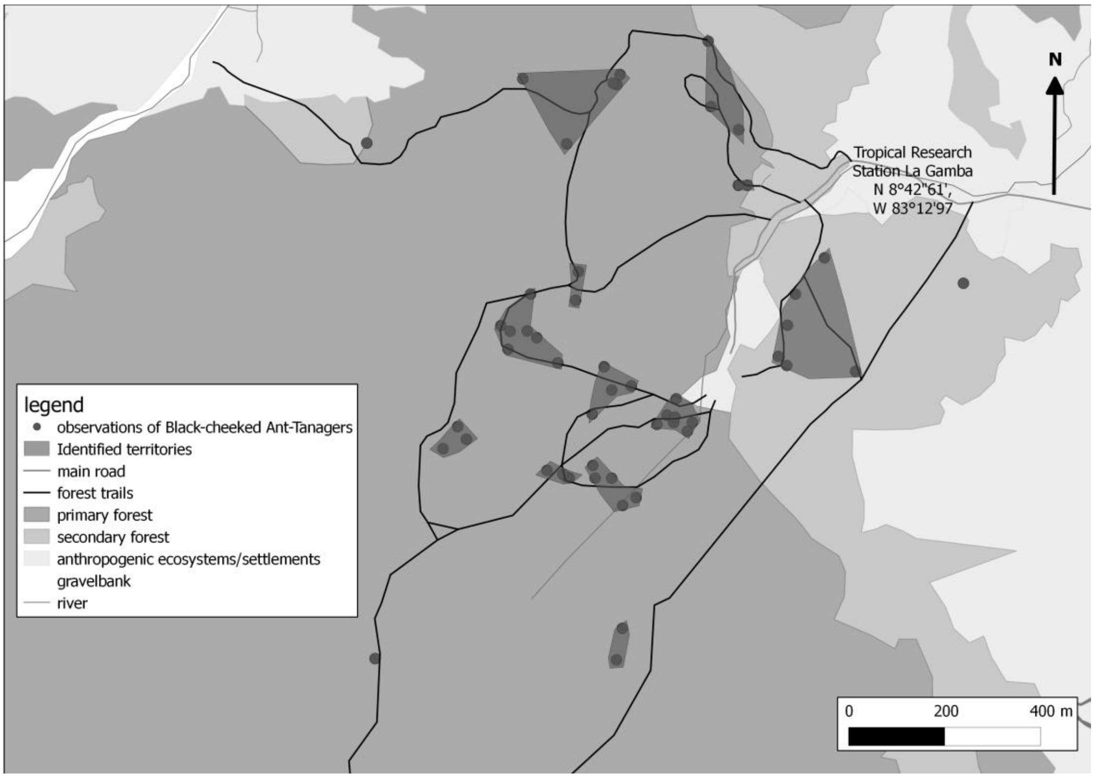

Figure 6. Observations of Black-cheeked Ant-Tanagers and their affiliation to identified territories in vicinity to the Tropical Research Station La Gamba in 2010/2011.

Discussion

The Black-cheeked Ant-Tanager – a forest interior species

As emphasized earlier (Aubrecht, 2008; BirdLife International, 2012), our study clearly showed that the occurrence of the Black-cheeked Ant-Tanager is restricted to the interior and margin of primary and old-growth secondary forest. The species does not move into younger secondary forests and gallery forest strips, even when they are connected to closed forest. Although the Black-cheeked Ant-Tanager can be frequently found close to the forest margin (this study; Seaman & Schulze, 2010), our data showed that its occurrence at forest census points was positively related to the percentage of forest cover within a radius of 200 m. This indicates that the species tends to avoid forest edges. The species' preference for old-growth largely undisturbed forest is further emphasized by our finding that its likelihood of occurrence increased with increasing canopy closure and density of large trees. This is in contradiction to Slud (1964), who noted, that the species prefers tall second growth and broken forests to the interior of unbroken forests. Furthermore, it remains doubtful if occasional observations of birds in beachfront scrub and palms adjacent to Corcovado National Park (Capper et al., 1998) or in other disturbed habitats at the margin of closed forests (e.g. the botanical garden of the Tropical Research Station La Gamba; own observations) refer to territorial birds. More likely such records may refer to dispersing birds or individuals only occasionally exploiting attractive resources in habitats at the forest margin, which otherwise may be unsuitable for the species.

Population density estimates using distance sampling

Distance sampling is a method widely used to estimate the population density of species in challenging field conditions (Thomas et al., 2010). It is frequently applied to estimate the population density of endangered low density species (e.g. Heydon & Bulloh, 1997; Morrogh-Bernard et al., 2003; Hoekman et al., 2011) including understory forest birds (e.g. Jiménez et al., 2003; Shankar Raman, 2003). During both of our survey periods the number of Black-cheeked Ant-Tanager observations was higher than about 50, the minimum number of detections recommended for estimating population densities with the software Distance (Buckland et al., 1993; but see Oostra et al., 2008).

Our distance sampling data from the survey period 2010/2011 does not indicate that the number of detected birds in the first distance band was affected by the forest trails which were used as transect line. Additionally, the trail did obviously not act as barrier for bird movements. Frequently, Black-cheeked Ant-Tanagers were observed crossing the small paths (own observations). In contrast, the distribution of measured detection distances from the survey in 2009 (and in consequence the data combining distances sampled in 2009 and 2010/2011) is characterized by an overrepresentation of records in the first distance band and less observed birds than expected in the second distance band. However, we do not believe that the unexpected high number of Black-cheeked Ant-Tanagers detected in the first distance band during the 2009 distance sampling is caused by using forest trails as transect lines. Rather, it may be a result of territorial behavior during the species' breeding season which lasts from mid January to May (Sandoval & Gallo, 2009), the time period of our 2009 survey (February-April). During the breeding season birds may approach an observer entering their territory more frequently and, therefore, may move more often towards the transect line before detection.

The 2010/2011 detection curves had a high detection rate from the zero line up to over ten meters and then decreased rapidly. The resulting relatively broad shoulder is a feature essential for the accuracy of population density estimation (Buckland et al., 1993). For this reason the population density estimated by distance sampling for the survey 2010/2011 may be more reliable. However, in fact, both estimates for 2010/2011 and 2009 correspond well to the densities estimated by the number of territories identified in our study area in 2010/2011 (this study) and 2009 (Fricke and Katz, unpublished).

Population density estimated by territory mapping

Based on territory mapping in 2010/2011, a total of 12 breeding pairs was estimated for our study area, which corresponds to 17-25 individuals in our 1.45 km^2 study area when assuming 2-3 birds per family group (Aubrecht, 2008). Also in 2009 the density predicted by distance sampling (21-24 birds) was similar to the one achieved by territory mapping (eight territories ≈ 16-24 individuals; Fricke and Katz, unpublished).

Other studies (e.g. Gale et al., 2009; Gottschalk & Huettmann, 2011; Shankar Raman, 2003) comparing territory mapping with point or line distance sampling methods in tropical forests as well as in forests and open landscapes in the temperate zone showed that territory mapping produced similar results similar than the less work intensive line distance sampling (Gottschalk & Huettmann, 2011; Shankar Raman, 2003).

The spatial distribution of territories identified in 2009 (Fricke and Katz, unpublished) and 2010/2011 (this study) was remarkably similar. Several 2009 and 2010/2011 territories overlapped or were located in close distance to each other. This could indicate a minor turnover of territory owners or that territory sites have to fulfill specific requirements. A low turnover of territory owners and a rather stable spatio-temporal pattern of territories was already recorded for other understory rainforest birds (Greenberg & Gradwohl, 1986).

Comparison with previous population size estimates

Based on the assessment of known records, descriptions of abundance and range size, the current population size estimated by the IUCN for the Black-cheeked Ant-Tanager is about 10,000-19,999 individuals (BirdLife International, 2012). However, on the provided distribution map the species is marked as possibly extinct in the area of the Piedras Blancas National Park (IUCN, 2012). In fact, our study documented that the species appears to be still abundant in Piedras Blancas National Park. Therefore, when assuming that the species occurs in any old-growth forest in all three protected areas, Corcovado National Park, Golfito Faunal Refuge and Piedras Blancas National Park, the actual distribution range may cover an area of about 592 km^2. Considering an average density of between 24 and 27 individuals per km^2 (as estimated by our distance sampling study), the current population size may be between 12,432 and 20,720 birds.

Conservation implications

Because the remaining distribution range of the Black-cheeked Ant-Tanager is exclusively located within protected areas of Pacific lowland rainforest, the species can be classified as actually not threatened by extinction. If the species has indeed a decreasing population trend (BirdLife International, 2012) has to be verified by a monitoring of its remaining populations. In particular, the species' actual status in the Golfito Faunal Reserve in vicinity of Golfito has to be assessed (Wege & Long, 1995). Further sites, which should be surveyed for remaining populations, include the forest area of the Golfo Dulce Forest reserve (protection category five; IUCN criteria).

As documented by our study, Black-cheeked Ant-Tanagers tend to avoid forest edges and do not appear to move into more disturbed forests. This is emphasizing, that any further forest disturbance and fragmentation within its remaining distribution range will most likely result in local extinctions. These local extinctions can hardly be compensated by re-colonization. Even gallery forest strips connecting remaining forest fragments, thereby helping to improve landscape connectivity for several forest species (Seaman & Schulze, 2010), apparently do not represent a promising conservation tool to facilitate mobility of Black-cheeked Ant-Tanagers. Like for other forest specialists the full protection of the remaining lowland forest at the southern Pacific slope will remain the only way to successfully protect its unique avifauna. Costa Rica has a high reputation for preserving its biodiversity and is setting standards for conservation networks (13.74% of the country is strictly protected), which play an important role for the protection of threatened species (Sánchez et al., 2009). Hopefully, also the endemic Black-cheeked Ant-Tanager will benefit from this conservation policy exemplary for tropical countries!

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